

A REVISION OF THE FOSSIL MEGAPODIIDAE (AVES), INCLUDING A DESCRIPTION OF A NEW SPECIES OF *PROGURA* DE VIS

by G. F. VAN TETS*

Summary

VAN TETS, G. F. (1974).—A revision of the fossil Megapodiidae (Aves), including a description of a new species of *Progura* De Vis. *Trans. R. Soc. S. Aust.* 98(4), 213-224, 30 November, 1974.

Long bones of two fossil species of megapodes are described from Pleistocene deposits from south-eastern Australia. Both species are much larger than extant species of megapodes. The larger of the two, *Progura gallinacea* De Vis, 1888a, was described and classified as a crowned pigeon, Columbidae; as an undetermined bustard, Otididae (De Vis 1888b); as a megapode, *Chosornis praeteritus* De Vis, 1889; and as a stork, *Palaeopelargus nobilis* De Vis, 1891.

The smaller of the two is named *Progura naracoortensis* n. sp. It differs from its congener by having a relatively shorter tarsometatarsus.

Of other megapodes, fossil remains have been found only of one specimen of *Leipoa ocellata*, Malleefowl, and of one or more indeterminable juvenile megapodes. Fossil remains reported, as those of *Alectura lathamii*, Brush-turkey, are of *Progura gallinacea* and *P. naracoortensis*.

Introduction

Brodkorb (1964, p. 307) mentions only two fossils in the Megapodiidae, a carpometacarpus which is the holotype of *Chosornis praeteritus* De Vis, 1889, and a coracoid which Lydekker (1891) determined as that of a large gallinaceous bird and provisionally referred to *Alectura lathamii* J. E. Gray, 1831, Brush-turkey. A tarsometatarsus, closely comparable with that of *A. lathamii*, was reported by Longman (1945).

Recently more fossil material of megapodes was located in south-eastern Australia, including remains of an undescribed species. These, and four tarsometatarsi, the syntypes of *Progura gallinacea* De Vis, 1888a, are here re-assigned to the Megapodiidae. *Progura* was placed by De Vis in the Columbidae near the crowned pigeons (*Goura* Stephens, 1819). De Vis (1888a) considered both *Progura* and *Goura* to be close to the common ancestor of poultry and pigeons.

In this paper the new species is described, and the long bones of fossil megapodes are compared with those of extant megapodes (*Megapodius pritchardi* G. R. Gray, 1864,

Niuafoou Fowl; *M. (freycineti) reinwardti* Dumont, 1823, Scrubfowl; *Alectura lathamii*, Brush-turkey; and *Leipoa ocellata* Gould, 1840, Malleefowl); and of crowned pigeons (*Goura scheepmakeri* Finsch, 1876, and *G. victoria* (Fraser, 1844)).

Methods

The study material was made available by the following museums and is identified in the text by their initials and numbers: Australian Museum, Sydney (AM); British Museum (Natural History), London (BMNH); National Museum of Victoria, Melbourne (NMV); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); United States National Museum, Washington (USNM); and CSIRO, Division of Wildlife Research, Canberra (CSIRO).

The terminology of Harvey *et al.* (1968) is used for bones and their parts. Examples of fossil bones are figured together with a corresponding bone of a Scrubfowl. Mirror images of some bones have been drawn, so that all bones on a figure appear as if they are from the same side.

* Division of Wildlife Research, CSIRO, P.O. Box 84, Lynnham, A.C.T. 2602.

Measurements of the bones were made as recommended by Scarlett (1972) and Schnell (1970) and as indicated on the figures. They include: length; width at proximal or dorsal end; width at narrowest point on shaft; and width at distal or ventral end. On the carpo-metacarpus, the greatest and least width of the proximal end was measured in accordance with De Vis (1889), and the greatest and least width at the narrowest point on the shaft of metacarpal III. On the tarsometatarsus, the width below the articular impression of the first metatarsal or hallux and the width of the central trochlea was measured. On the scapula the width of the blade was measured.

Weights of Malleefowl were obtained from the records of the CSIRO Bird-Banding Scheme, and weights of Scrubfowl from the labels on specimens in the collections of the Western Australian Museum, Perth and the Division of Wildlife Research, Canberra.

Material and Synonymy of *Progora gallinacea*

Progora gallinacea De Vis, 1888: 131.

Chosornis praeteritus De Vis, 1889: 55.

Palaeopelargus nobilis De Vis, 1891: 441 (new synonymy).

The syntypes of *Progora gallinacea* De Vis, 1888a, are those De Vis figured on Plate VI, two proximal parts of left tarsometatarsi (QM, F1134 and F1143) and two distal parts of right tarsometatarsi (QM, F5556-7). Because the syntypes are complementary fragments of the tarsometatarsus I have not selected a lectotype.

De Vis (1889) in his description of the holotype of *Chosornis praeteritus*, refers to "the metacarp of the left manus", but he figures on Plate IV a proximal part of a right carpo-metacarpus which is now numbered QM, F1132. Another proximal part of a right carpo-metacarpus bore the same number, but has been renumbered QM, F7005. It is more worn than QM, F1132 and is not the one figured on Plate IV. The description could pertain to either specimen. QM, F1132 should be regarded as the holotype of *Chosornis praeteritus* and the reference to "the left manus" should be dismissed as a *lapsus calami*.

A distal part of a right carpo-metacarpus (QM, F1139) is figured by De Vis (1891) on Plate 24 as the holotype of a stork, *Palaeopelargus nobilis*, Ciconiidae. Pat Vickers Rich and I found the holotypes of *Chosornis praeteritus* and of *Palaeopelargus nobilis* (QM,

F1132 and F1139) to be matching fragments of the same bone.

Referred Specimens: The following material agrees in size with the type of *Progora gallinacea*. In shape, all specimens resemble the corresponding parts of extant megapodes, but they are very much larger in size. *Progora gallinacea* is the oldest available name for them. They are: the material of *Chosornis praeteritus* (QM, F1132 and F7005); the material of *Palaeopelargus nobilis* (QM, F1139), and a distal part of a right ulna (QM, F5553) (referred by De Vis (1891)); a proximal part of a right scapula (QM, F5558) (figured on Plate 35 and referred to the Otididae as an undetermined genus and species of bustard by De Vis (1888b)); an almost complete left coracoid (BMNH, A3244) (*Talgalla lathamii* 43879 of Lydekker (1891)); an almost complete right coracoid (AM, F54720); a proximal part of a right ulna (AM, F54721); distal parts of two right ulnas (AM, F54722-3); a proximal part of a left tarsometatarsus (AM, F54724); a distal part of a left tarsometatarsus (AM, F54725); a distal part of a right tarsometatarsus (AM, F54726); and an incomplete distal part of a right tarsometatarsus (AM, F7033) (formerly also numbered QM, F1134).

Description of *Progora naracoortensis* n.sp.

Though the following material resembles corresponding parts of extant megapodes in shape, it is intermediate in size between *P. gallinacea* and extant megapodes. The material is consistent in size. The most distinctive bone is an almost complete right tarsometatarsus (SAM, P17856). It is not only smaller, but its relative length is also very much shorter than that of the syntypes of *P. gallinacea*.

Holotype: I have therefore selected SAM, P17856 as the holotype of *Progora naracoortensis* n.sp. It is named after Naracoorte, South Australia, where the holotype and most of the other remains of *P. naracoortensis* were found.

Referred specimens: The proximal part of a left tarsometatarsus (QM, F2769) was reported by Longman (1945) as closely comparable with that of a Brush-turkey. In size and shape it looks like a mirror image of SAM, P17856, the holotype of *P. naracoortensis*.

Further material of *P. naracoortensis* consists of an almost complete right coracoid (SAM, P16700); a complete and two distal

ends of left humeri (SAM, P17153-4 and P17878); a proximal and a distal part of a right humerus (SAM, P18183); an almost complete right ulna (SAM, P17877); and two distal parts of left ulnae (SAM, P17879 and P18182); a complete left radius (SAM, P18184); a proximal part of a right femur (SAM, P17857); a distal part of a right femur (SAM, P18186); a complete right tibiotarsus (SAM, P17152); a distal part of a right tibiotarsus (SAM, P17876); a proximal part of a right tarsometatarsus (SAM, P18185); a cervical vertebra (SAM, P18181); and an anterior fragment of a synsacrum (SAM, P18187).

Fossil remains of other megapode species

Compared to *Progora* very few fossil remains have been found of other megapodes. As explained above, specimens reported as *Alectura lathami* by Lydekker (1891) and Longman (1945), are also *Progora* remains, and there are no other known fossil remains of the Brush-Turkey.

Fragments of a cranium of a Malleefowl (SAM, P16738) were found in the same deposit with the following remains of one or more juvenile megapodes of similar size but of indeterminable genus and species: a premaxilla (SAM, P16739), a sternum (SAM, P16740); a proximal part of a right ulna (SAM, P16741); a proximal part of a left femur (SAM, P16742); a distal part of a right femur (SAM, P16743); a distal part of a left tibiotarsus (SAM, P16744); and an almost complete right tibiotarsus (SAM, P16745).

Age and distribution of fossil megapodes

The following fossils of megapodes have been found in Pleistocene deposits in south-eastern Australia. None have been found in association with human remains nor with those of dogs and other domestic and feral animals. The map (Fig. 1) has been adapted from Frith (1962).

South-eastern Queensland

The syntypes of *Progora gallinacea* (QM, F1134, F1143 and F5556-7) and *P. gallinacea* (QM, F7033) were collected at Ravensthorpe near Pilton, Darling Downs (27°54'S, 152°10'E). According to a label associated with QM, F7033, it was collected on '11-9-1888' by R. W. Frost. QM, F1132, the holo-

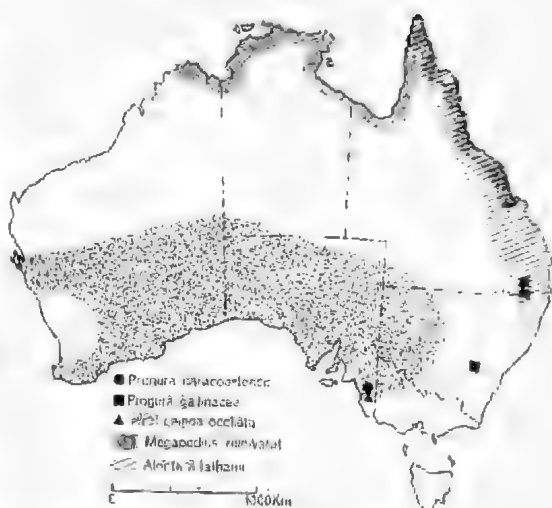


Fig. 1. Distribution of fossil and extant megapodes in Australia.

type of *Chosornis praeteritus*, and QM, F5558 were, according to labels associated with the specimens, collected at Chinchilla, Darling Downs (26°45'S, 150°40'E). The holotype of *Palaeopelargus nobilis* (QM, F1139), QM, F5553 and QM, F7005 are from unknown localities in the Darling Downs.

P. naracoortensis (QM, F2769) was collected on 24 May, 1945, by E. T. O'Rourke at the Gore Limestone Quarries (28°18'S, 151°30'E) (Longman 1945).

Eastern New South Wales

The first material to be collected of *P. gallinacea* (BMNH, A3244), was obtained from a cave in the Wellington Valley near Wellington (32°35'S, 148°55'E), and was presented in 1870 to the British Museum (Natural History) by the Trustees of the Australian Museum (Lydekker 1891). Another specimen of *P. gallinacea* (AM, F54723) was collected from one of the Walli Caves in the Wellington Valley in 1966 or 1967 by R. M. Frank¹. Jeanette Hope found *P. gallinacea* (AM, F54720-2, and F54724-6), in the one lump of matrix at the Wombeyan Quarry of Industrial Rock Mines Ltd. about 1½ km west of Wombeyan Caves Reserve (34°19'S, 149°56'E), in April 1970. They may be of a single individual which appears to have fallen down a vertical entrance shaft and to have been crushed by subsequent deposits.

¹ Frank, R. M. (1972).—Sedimentological and morphological study of selected cave systems in eastern N.S.W., Australia, Ph.D. thesis, A.N.U. (unpublished).

South-eastern South Australia

The holotype of *Progora naracoortensis* (SAM. P17856), as well as *P. naracoortensis* (SAM. P17152-4, P17857, P17876-9, and P18181-7) were collected at Henschke's Quarry Cave near Naracoorte (37°00'S, 140°45'E) by Mr. F. Aslin. Sample SUA243 from Henschke's Quarry Cave has a radio-carbon date of about 33,800 BP (N. Pledge, pers. comm.). *P. naracoortensis* (SAM. P16700) was collected by Dr. R. T. Wells and other members of the Cave Exploration Group of South Australia at Victoria Cave near Naracoorte, together with Malleefowl (SAM. 16738) and juvenile megapode(s) (SAM. P16739-45).

Comparisons of long bones of megapodes and crowned pigeons

Coracoid

The coracoids of *Goura* have relatively broader dorsal and ventral ends than those of megapodes. The coracoids of the species of megapodes differ mainly in length (see Table 1 and Fig. 2).

Scapula

The scapulae of megapodes and other galliform birds have a scapular tubercle. This tubercle does not occur in most other kinds of birds including Otidiidae and *Goura*. The glenoid facet is round in *Goura* and is quadrangular in Otidiidae and Megapodiidae. The long axis of the glenoid facet is parallel to the shaft in Otidiidae and at right angles to the shaft in Megapodiidae.

The scapula of *P. naracoortensis* is not known. The scapulae of the species of megapodes differ in size (see Table 2 and Fig. 2).

Humerus

The humeri of *Goura* are relatively shorter, more massive and have more prominent deltoid crests than those of megapodes. The humerus of *P. gallinacea* is not known. The humeri of the species of megapodes differ mainly in length (see Table 3 and Fig. 3).

Ulna

The ulnae of *Goura* are straighter and have more prominent feather bases than those of megapodes. The ulnae of the species of megapodes differ in size, except for an overlap in length between Scrubfowl and Brush-turkey (see Table 4 and Fig. 3).

TABLE 1

Measurements of Coracoids of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Dorsal Width mm	Shaft Width mm	Ventral Width mm
<i>P. gallinacea</i>	BMNH, A7244		L			10	
	AM. F54/20		R	94		10	30
<i>P. naracoortensis</i>	SAM. P16700		R	85	18	10	24
<i>G. victoria</i>	NMV. W6676		L	85	19	9	25
			R	83	19	9	25
<i>G. scheepmakeri</i>	NMV. R8054		L	78	17	9	26
			R	78	17	9	25
<i>L. ocellata</i>	SAM. B11482	♂	L	64	14	6	18
			R	63	13	6	18
	SAM. B24306	♀	L	64	14	6	18
			R	64	14	6	19
	SAM. B3039	♀	L	62	14	6	19
			R	62	14	6	20
	NMV. B9276		L	64	14	6	17
			R	66	13	7	18
<i>A. lathami</i>	NMV. W4964		L	60	11	6	15
			R	60	11	5	15
	NMV. W4554		L	61	11	5	16
			R	61	11	5	17
	NMV. W4554		L	60	12	5	15
			R	59	11	5	15
<i>M. reinwardi</i>	CSIRO.						
	GALS 2	♂	L	54	12	5	17
			R	54	12	5	17
	CSIRO.						
	GALS 3	♂	L	55	11	5	13
			R	55	11	5	13
<i>M. griseiceps</i>	USNM. 319634		L	37	7	3	10
			R	37	7	3	10

Radius

The radii of *Goura* are arched upwards and those of megapodes are arched forwards.

The radii of the species of megapodes differ in size except for an overlap in length between Scrubfowl and Brush-turkey (see Table 5 and Fig. 3).

Carpometacarpus

The carpal II process of *Goura* is relatively larger and more prominent than that of megapodes. De Vis (1889) noted the absence of an intermetacarpal process in the holotype of *Chosornis praeteritus*. This process is a prominent structure in the Passeriformes and the Northern Hemisphere based galliform families, Phasianidae, Tetraonidae and Meleagridae. It is absent in the Columbigiformes including *Goura* and the Southern Hemisphere based galliform families, Megapodiidae, Cracidae and Numididae. The carpometacarpus of *P. naracoortensis* is not known. The carpometacarpi of the species of

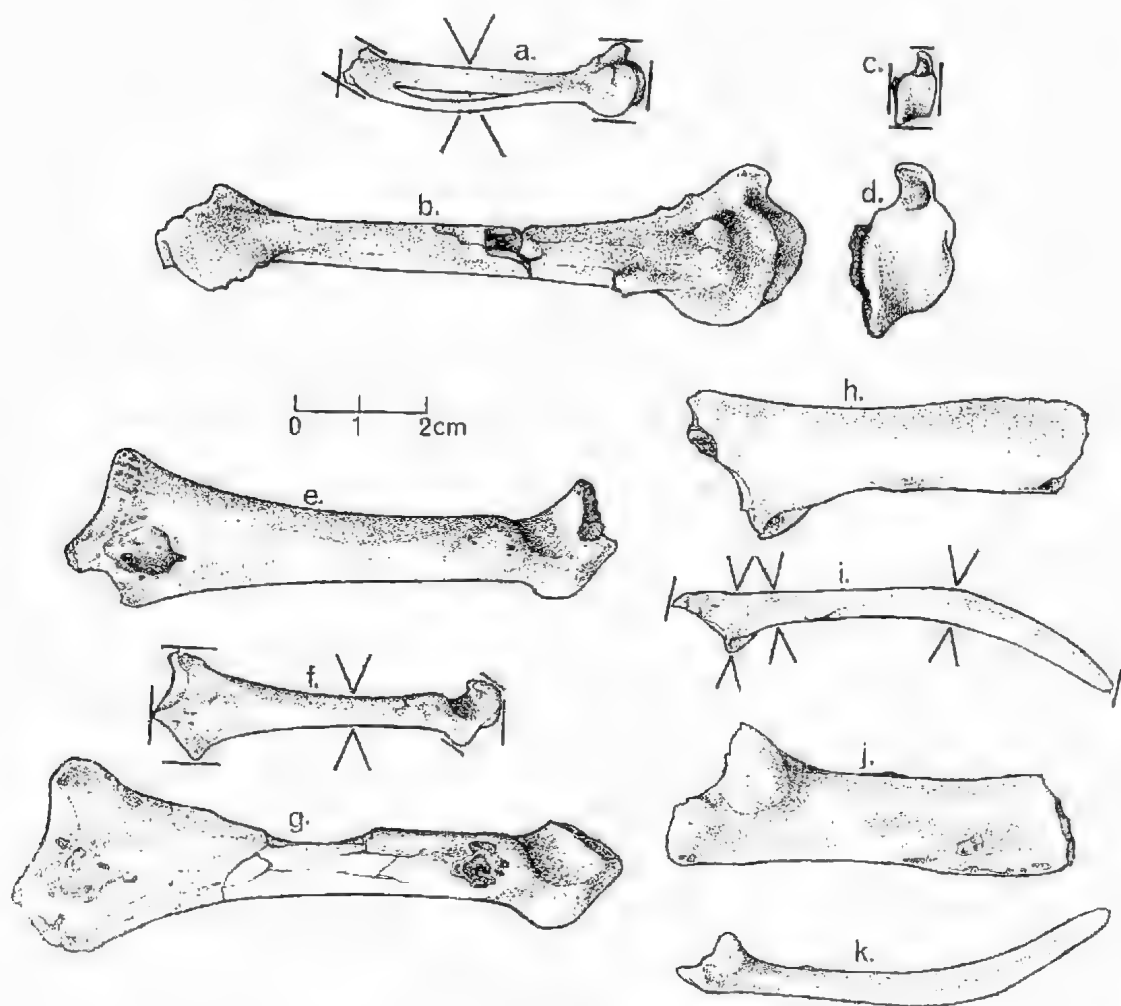


Fig. 2. a. and c.—right carpometacarpus, *M. reinwardt* (CSIRO, GALS3); b. and d.—right carpometacarpus, *P. gallinacea* (QM, F1132 and F1139); e.—right coracoid, *P. naracoortensis* (SAM, P16760); f.—right coracoid, *M. reinwardt* (CSIRO, GALS3); g.—right coracoid, *P. gallinacea* (AM, F54720); h. and j.—right scapula, *P. gallinacea* (QM, F5558); i. and k.—right scapula, *M. reinwardt* (CSIRO, GALS3).

megapodes differ in size, except for an overlap in length between Scrubfowl and Brush-turkey (see Table 6 and Fig. 2).

Synsacrum

The synsacra of *Goura* have a median ventral ridge at the anterior end. This ridge does not occur in megapodes. The synsacra of megapodes differ in size (see Fig. 4).

Femur

The shaft is narrowest distally in *Goura* and proximally in megapodes. The trochanteric

ridge is more pronounced in megapodes than in *Goura*. The femur of *P. gallinacea* is not known. The femora of the species of megapodes differ in size except for an overlap in length between Malleefowl and Brush-turkey (see Table 7 and Fig. 4).

Tibiotarsus

The tibiotarsi of *Goura* lack a prominent notch on the medial condyle which is present in megapodes. The tibiotarsus of *P. gallinacea* is not known. The tibiotarsi of the species of megapodes differ in size except for an overlap

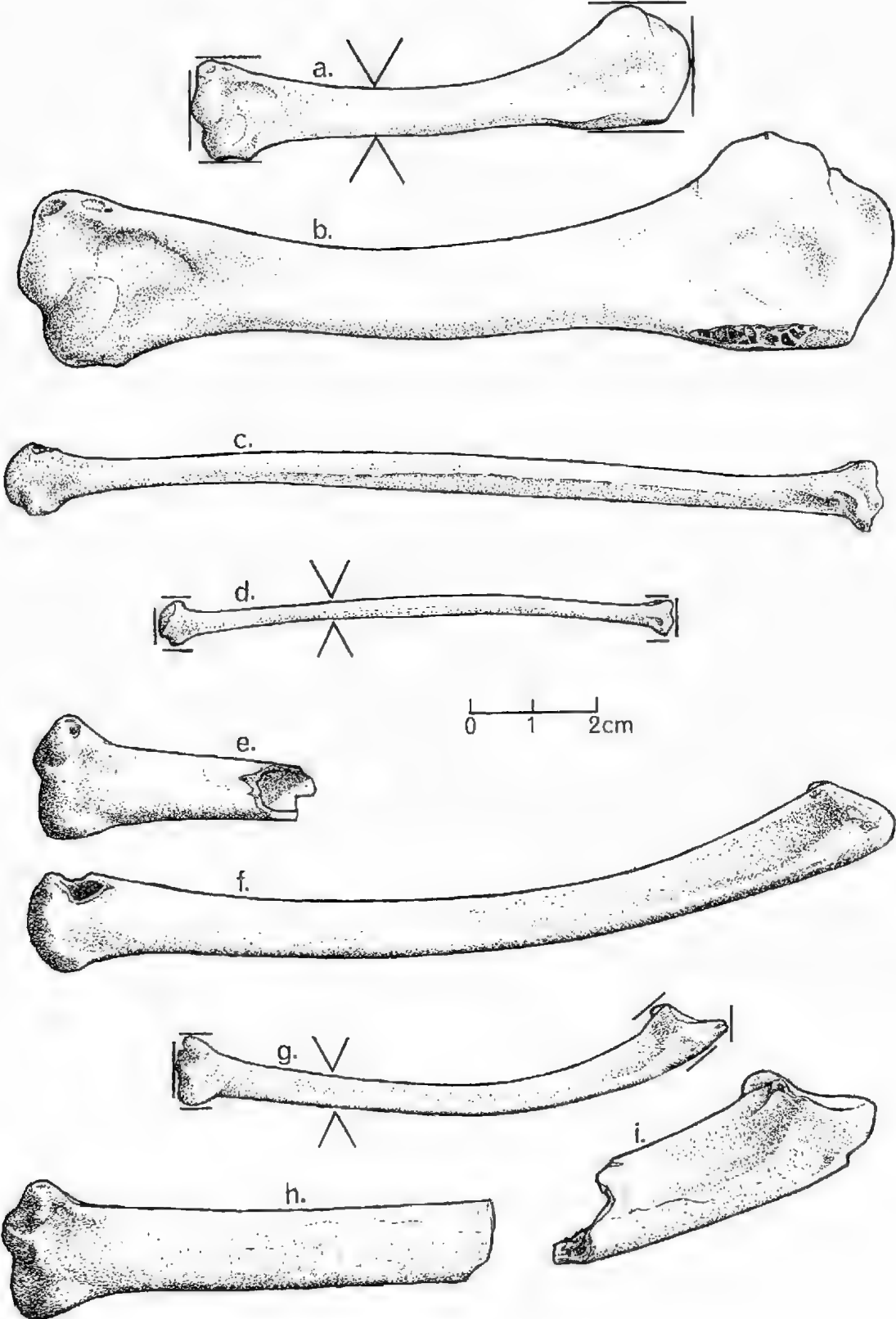


TABLE 2

Measurements of Scapulae of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal Width mm	Shaft Width mm	Blade Width mm
<i>P. gallinacea</i>	QM, F5558		R		22	14	
<i>G. victoria</i>	NMV, W6676		L	86	14	7	12
			R	87	14	7	11
<i>G. scheepmakeri</i>	NMV, R8054		L	87	13	6	12
			R	88	12	6	13
<i>L. ocellata</i>	NMV, B9276		L	79	12	6	10
			R	80	12	6	10
<i>A. lathamii</i>	NMV, W5964		L	79	10	6	9
			R	77	10	6	9
	NMV, W4554		L	78	10	5	9
			R	77	10	5	9
	NMV, W4555		L	75	9	5	8
			R	75	10	5	8
<i>M. reinwardi</i>	CSIRO, GALS 2	♂	L	68	9	5	6
			R	68	10	5	7
	CSIRO, GALS 3	♂	R	69	9	5	6
<i>M. pritchardi</i>	USNM, 319634		L	48	6	3	4
			R	48	6	3	4

in length between Malleefowl and Brush-turkey (see Table 8 and Fig. 4).

Tarsometatarsus

The articular impression of the 1st metatarsal is prominent in megapodes and inconspicuous in *Goura*. The shaft is narrow below the impression in *Goura* and broad in megapodes. The hypotarsus is more slender and finely formed in *Goura* than in megapodes. The tarsometatarsi of the species of megapodes differ in size (see Table 9 and Fig. 4).

Relative bone lengths

In Table 10, the lengths of the limb bones are expressed in terms of coracoid lengths. *Goura* differs by having relatively shorter humeri, femora and tibiotarsi, than megapodes. The tarsometatarsi of *Goura*, *P. naracoortensis* and *L. ocellata* are relatively shorter than those of *P. gallinacea*, *A. lathamii*, *M. reinwardi* and *M. pritchardi*.

TABLE 3

Measurements of Humeri of Megapodes and Crowned Pigeons

Species	Number	Sex/Age	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. naracoortensis</i>	SAM, P17153		L	144	36	14	30
	SAM, P17154		L				32
	SAM, P18183		R		39	15	32
	SAM, P17878	+	L			13	26
<i>G. victoria</i>	NMV, W6676		L	108	34	12	25
			R	108	33	12	25
<i>G. scheepmakeri</i>	NMV, R8054		L	101	30	11	23
			R	102	30	11	23
<i>L. ocellata</i>	SAM, B11482	♂	L	100	22	8	19
			R	101	22	8	19
	SAM, B5039	♀	L	102	24	9	19
			R	103	24	8	19
	NMV, B9276		L	107	23	9	19
			R	108	24	9	20
<i>A. lathamii</i>	NMV, W5964		L	87	21	9	18
			R	86	20	8	18
	NMV, W4554		L	90	21	8	18
			R	90	21	8	18
	NMV, W4555		L	88	21	8	18
			R	89	21	8	18
<i>M. reinwardi</i>	CSIRO, GALS 2	♂	L	82	19	8	15
			R	82	19	8	16
	CSIRO, GALS 3	♂	L	83	19	8	17
			R	84	19	9	16
<i>M. pritchardi</i>	USNM, 319634		L	59	12	4	11
			R	59	12	4	11

* Juvenile.

Weights

Weights of seven male Malleefowl ranged from 2.0 to 2.2 kg and of four females from 1.8 to 1.9 kg. Weights of five male Scrubfowl ranged from 0.8 to 1.2 kg and of seven females from 0.6 to 1.1 kg. Maschanka (1972) found no significant sexual differences in the bone lengths of Malleefowl, and Sutter (1965) found that of three Brush-turkey raised in captivity, two females reached weights of 2.0 and 2.1 kg and a male 2.5 kg. This limited evidence suggests that male megapodes are only slightly larger than females.

If it is assumed that weight is proportional to the cube of the length of the coracoid and that the average weight of Malleefowl is two

Fig. 3. a.—left humerus, *M. reinwardi* (CSIRO, GALS3); b.—left humerus, *P. naracoortensis* (SAM, P17153); c.—left radius, *P. naracoortensis* (SAM, P18184); d.—left radius, *M. reinwardi* (CSIRO, GALS3); e.—left reversed ulna, *P. naracoortensis* (SAM, P17879); f.—right ulna, juvenile *P. naracoortensis* (SAM, P17877); g.—right ulna, *M. reinwardi* (CSIRO, GALS3); h. and i.—right ulna, *P. gallinacea* (AM, F54721 and F54722).

TABLE 4

Measurements of Ulnae of Megapodes and Crowned Pigeons

Species	Number	Sex/Age	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. gallinacea</i>	QM, F5553		R			11	20
	AM, F54721		R		23		
	AM, F54722		R			12	22
	AM, F54723		R			11	22
<i>P. naracoortensis</i>	SAM, P17879		L			10	19
	SAM, P18182		L			10	19
	SAM, P17877	*	R	137	19	10	
<i>G. victoriae</i>	NMV, W6676		L	131	19	9	17
			R	131	18	8	17
			L	124	18	8	14
<i>G. scheepmakeri</i>	NMV, R8054		R	124	17	9	14
			L	103	14	7	13
			R	103	14	7	13
<i>L. ocellata</i>	SAM, B11482	Q ¹	L	106	15	6	13
	SAM, B5039	Q ¹	R	106	15	7	13
	NMV, B9276		L	111	14	7	12
			R	114	15	7	13
<i>A. lathamii</i>	NMV, W5964		L	89	13	7	12
			R	89	13	6	11
	NMV, W4554		L	88	13	7	11
			R	88	13	7	11
<i>M. reinwardi</i>	NMV, W4555		L	88	13	7	11
			R	88	13	6	11
	CSIRO, GALS 2	Q ¹	L	85	12	6	10
			R	85	12	6	10
<i>M. pritchardi</i>	CSIRO, GALS 3	Q ¹	L	87	13	5	11
			R	88	13	6	11
	USNM, 319634		L	67	8	4	7
			R	66	8	3	7

* Juvenile.

kg and of Scrubfowl one kg, then the weight of *P. gallinacea* would have been about five to seven kg and of *P. naracoortensis* about four to five kg.

A reconstruction of the relative sizes of the Australian megapodes is given in Fig. 5.

Power of flight

There are several kinds of birds that are over seven kg in weight and are capable of flying, e.g., turkeys, bustards, cranes and swans. The wing bones of the two *Progora* species are relatively and absolutely long and strong enough for them to have been capable of at least limited flight.

Ecology

Until more material, especially of the skull, of the species of *Progora* becomes available for study, very little can be said about how and in what habitats they lived. As large land

TABLE 5

Measurements of Radii of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. naracoortensis</i>	SAM, P18184		L	135	10	6	13
<i>G. victoriae</i>	NMV, W6676		L	120	9	5	10
			R	120	10	5	10
			L	114	7	5	10
<i>G. scheepmakeri</i>	NMV, R8054		R	114	9	5	10
			L	104	7	4	8
			R	105	7	4	8
<i>L. ocellata</i>	NMV, B9276		L	80	5	3	8
			R	79	6	3	8
			L	81	6	3	8
			R	80	6	3	8
<i>A. lathamii</i>	NMV, W5964		L	81	6	3	8
			R	81	6	3	8
			L	81	6	3	8
			R	81	6	3	8
<i>M. reinwardi</i>	CSIRO, GALS 2	Q ¹	L	79	6	3	8
			R	79	6	3	8
			L	60	6	3	7
			R	60	6	3	7
<i>M. pritchardi</i>	USNM, 319634		L	61	5	2	5
			R	61	4	2	5

TABLE 6

Measurements of Carpometacarpi of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. gallinacea</i>	QM, F1132		R	99	27 x 16	11 x 7	19
	QM, F1139		R		x 16-11 x 8		
	QM, F7005		R				
<i>G. victoriae</i>	NMV, W6676		L	69	21 x 12	7 x 5	12
			R	69	22 x 13	7 x 5	12
			L	64	21 x 11	7 x 5	14
<i>G. scheepmakeri</i>	NMV, R8054		R	65	19 x 12	7 x 5	14
			L	53	15 x 9	6 x 4	9
			R	54	15 x 9	6 x 5	9
<i>L. ocellata</i>	SAM, B11482	Q ¹	L	56	16 x 10	6 x 5	11
			R	55	16 x 10	6 x 5	9
			L	54	15 x 9	5 x 4	10
			R	54	16 x 9	5 x 4	10
<i>A. lathamii</i>	NMV, W5964		L	49	13 x 9	5 x 4	10
			R	49	12 x 8	5 x 4	9
			L	47	13 x 8	5 x 3	9
			R	47	13 x 8	5 x 3	9
<i>M. reinwardi</i>	NMV, W4555		L	46	13 x 8	5 x 3	9
			R	46	13 x 7	5 x 3	9
<i>M. pritchardi</i>	CSIRO, GALS 2	Q ¹	L	45	12 x 7	5 x 4	8
			R	46	12 x 7	5 x 4	8
			L	47	13 x 7	5 x 5	8
			R	46		5 x 4	8
<i>M. pritchardi</i>	USNM, 319634		L	53	7 x 4	3 x 2	5
			R	33	8 x 4	3 x 2	5

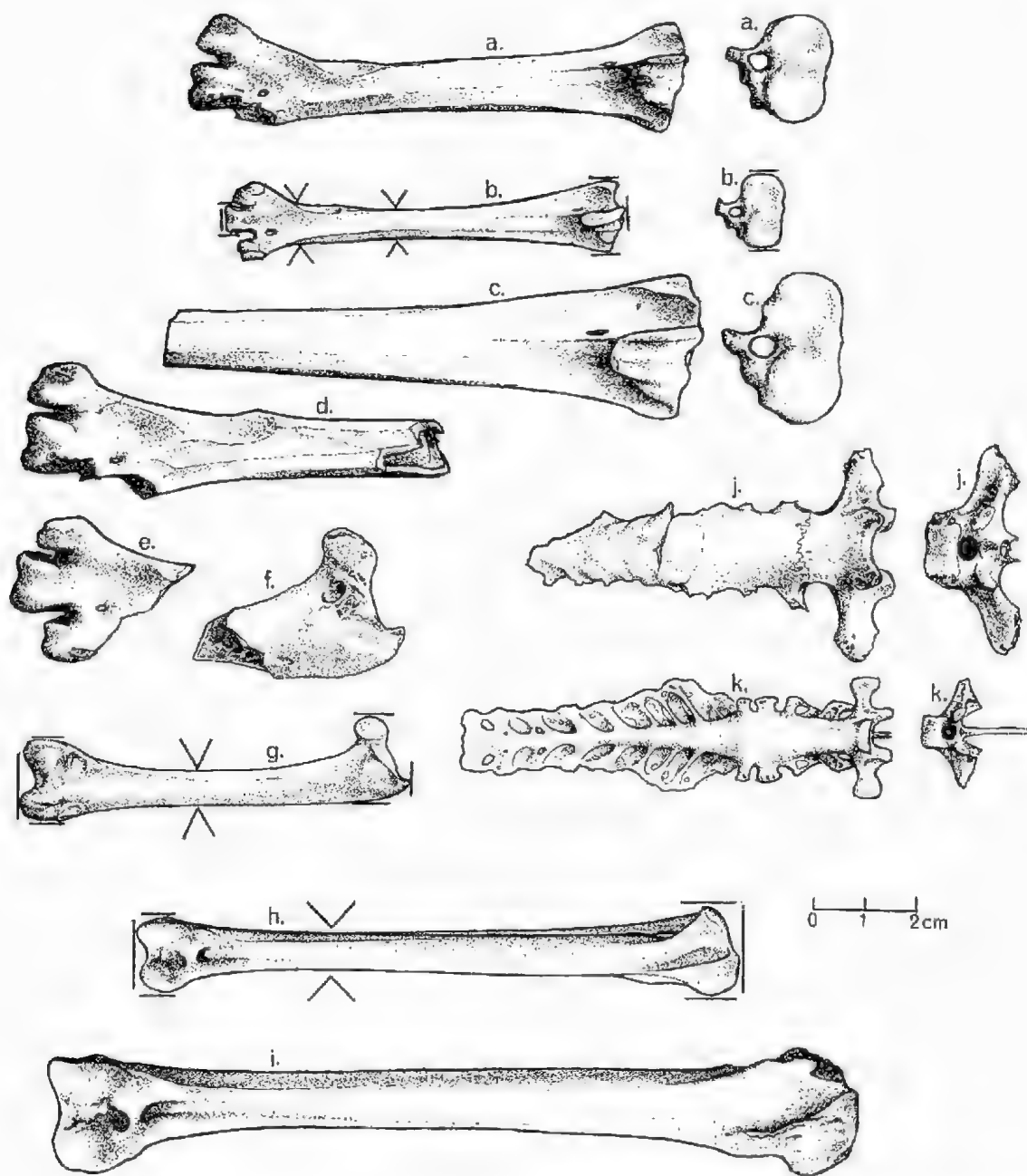


Fig. 4. *a.*—right tarsometatarsus, *P. naracoortensis* (SAM, P17856); *b.*—right tarsometatarsus, *M. reinwardt* (CSIRO, GALS3); *c.*—left reversed tarsometatarsus, *P. gallinacea* (QM, F1143); *d.* and *e.*—right tarsometatarsi, *P. gallinacea* (QM, F5556 and F5557); *f.*—right femur, *P. naracoortensis* (SAM, P17857); *g.*—right femur, *M. reinwardt* (CSIRO, GALS3); *h.*—right tibiotarsus, *M. reinwardt* (CSIRO, GALS3); *i.*—right tibiotarsus, *P. naracoortensis* (SAM, P17152); *j.*—synsacrum, *P. naracoortensis* (SAM, P18187); *k.*—synsacrum, *M. reinwardt* (CSIRO, GALS3).

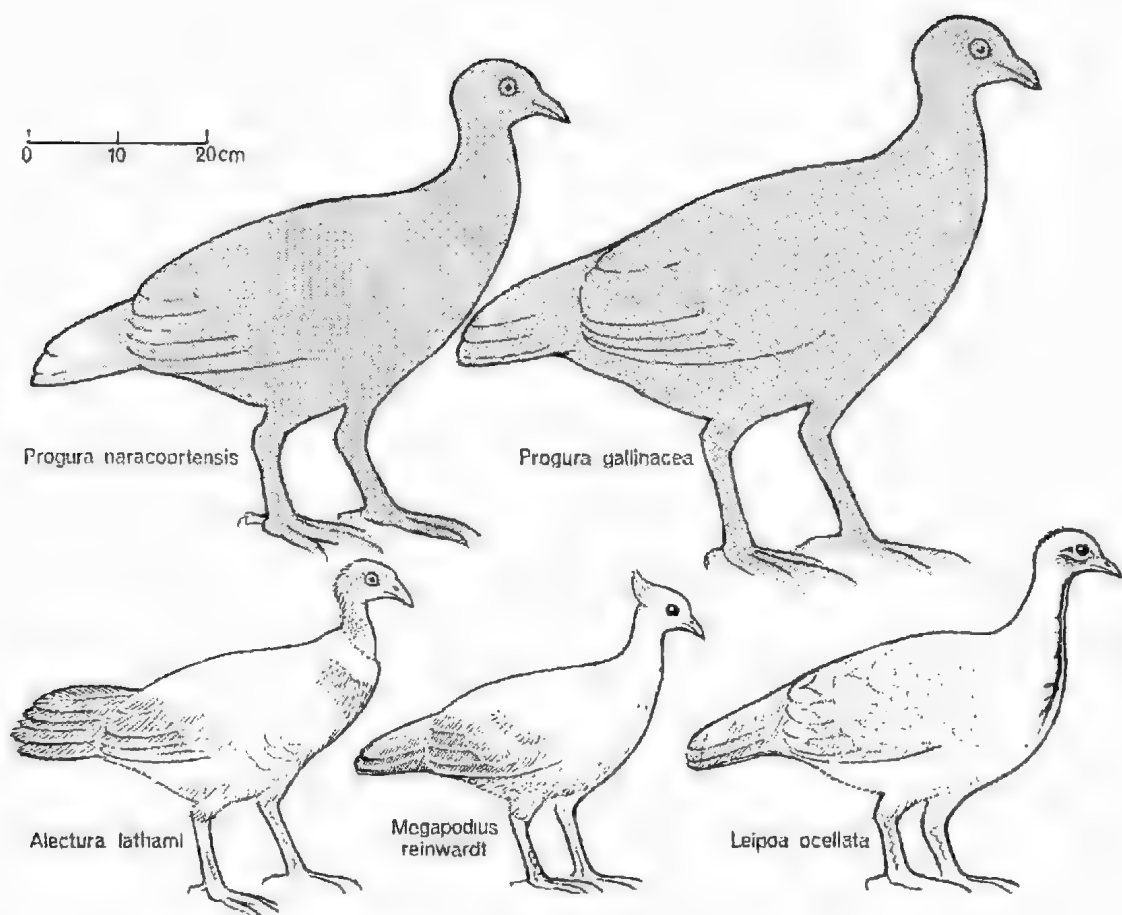


Fig. 5. Extant and reconstructed fossil megapodes of Australia.

birds, they presumably could survive in a wide range of habitats.

The relatively long legs of *P. gallinacea*, the Brush-turkey and the Scrubfowl suggest that *P. gallinacea* was also a rain forest species. Conversely the relatively short legs of *P. naracoortensis* suggest that it was an open shrub land bird like the Malleefowl. This assumption is supported by the discovery of remains of both of these latter species at Victoria Cave together with remains of other birds of open habitats (van Tets & Smith 1974).

Why the species of *Progura* died out may be related to the extinction of many other large vertebrates during the last peak in world glaciation. It may have been caused by environmental changes in Australia associated with increasing aridity, and with the displacement of native marsupial predators by men and dogs.

Systematics

The material of *Progura* indicates that there were two very large species of megapodes in south-eastern Australia, *P. gallinacea* and *P. naracoortensis*, during Pleistocene times. Other than size there are no clear characters that separate *Progura* from the other genera of megapodes nor that indicate to which of these genera it is closest. Relative tarsometatarsal lengths do indicate similarities between *P. naracoortensis* and *Leipoa* and between *P. gallinacea* and the other two Australian megapode genera, *Alectura* and *Megapodius*. Until further fossil material becomes available for study and there is a modern revision of the mainly monotypic megapode genera, it is preferable to use the genus *Progura* for the two fossil megapode species, *gallinacea* and *naracoortensis*.

TABLE 7

Measurements of Femora of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. naracoortensis</i>	SAM, P17857		R		30		
	SAM, P18186		R				28
<i>G. victoria</i>	NMV, W6676		L	88	21	8	19
			R	88	21	8	19
<i>G. scheepmakeri</i>	NMV, R8054		L	83	19	8	18
			R	83	19	8	18
<i>L. ocellata</i>	SAM, B11482	♂	L	84	20	8	19
			R	84	21	8	19
	SAM, B5039	♀	L	84	20	8	19
			R	84	21	9	19
	NMV, B9276		L	88	20	8	19
			R	90	20	8	19
<i>A. lathamii</i>	NMV, W5964		L	90	21	9	19
			R	90	21	9	19
	NMV, W4554		L	92	19	9	19
			R	92	19	10	19
	NMV, W4555		L	90	20	10	18
			R	89	20	9	18
<i>M. reinwardt</i>	CSIRO, GALS 2	♂	L	75	17	8	17
			R	75	17	8	17
	CSIRO, GALS 3	♂	L	77	17	7	17
			R	77	17	8	17
<i>M. pritchardi</i>	USNM, 319634		L	52	10	4	11
			R	52	10	4	11

TABLE 8

Measurements of Tibiotarsi of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal Width mm	Shaft Width mm	Distal Width mm
<i>P. naracoortensis</i>	SAM, P17152		R	158	25	11	23
	SAM, P17876		R			10	21
<i>G. victoria</i>	NMV, W6676		L	135	19	7	16
			R	135	20	7	16
<i>G. scheepmakeri</i>	NMV, R8054		L	126	17	7	14
			R	126	18	8	14
<i>L. ocellata</i>	SAM, B11482	♂	L	121	25	6	14
			R	121	25	6	14
	SAM, B5039	♀	L	123	22	6	13
			R	123	23	6	13
	NMV, B9276		L	130	21	7	15
			R	129	21	7	15
<i>A. lathamii</i>	NMV, W5964		L	129	20	8	14
			R	130	19	7	14
	NMV, W4554		L	135	19	7	14
			R	135	19	7	14
	NMV, W4555		L	134	18	7	14
			R	134	18	7	14
<i>M. reinwardt</i>	CSIRO, GALS 2	♂	L	114	19	7	13
			R	114	19	7	13
	CSIRO, GALS 3	♂	L	115	20	7	13
			R	115	19	7	12
<i>M. pritchardi</i>	USNM, 319634		L	84	12	4	8
			R	83	13	4	8

TABLE 10

Megapode and Crowned Pigeon bone lengths expressed as Coracoid lengths

Species	Humerus	Ulna	Radius	Carpo-metacarpus	Femur	Tibiotarsus	Tarso-metatarsus
<i>P. gallinacea</i>				1.1			1.6
<i>P. naracoortensis</i>	1.7	1.6	1.6			1.9	1.1
<i>G. victoria</i>	1.3	1.6	1.4	0.8	1.1	1.6	1.2
<i>G. scheepmakeri</i>	1.3	1.6	1.5	0.8	1.1	1.6	1.2
<i>L. ocellata</i>	1.6	1.6	1.6	0.9	1.3	1.9	1.2
<i>A. lathamii</i>	1.5	1.5	1.3	0.8	1.5	2.2	1.4
<i>M. reinwardt</i>	1.5	1.6	1.5	0.8	1.4	2.1	1.4
<i>M. pritchardi</i>	1.6	1.8	1.6	0.9	1.4	2.3	1.6

Acknowledgments

This paper owes a great debt to the many persons involved during the past century in collecting, cleaning and curating the bones that were made available for this study by the museums listed under methods.

I have benefitted greatly from discussions with colleagues in these museums and in CSIRO. In particular I am grateful to Jeanette Hope, Meredith Smith and Pat Vickers Rich who brought most of the undescribed fossil megapode material to my attention.

The figures were drawn by F. Knight.

TABLE 9

Measurements of Tarsometatarsi of Megapodes and Crowned Pigeons

Species	Number	Sex	Side	Length mm	Proximal width mm	Shaft width mm	Distal width mm	Shaft width below hallux mm	Central trochlea width mm
<i>P. gallinacea</i>	QM, F1134		Left		29				
	QM, F1143		Left		29	12			
	QM, F5556		Right	148		11		13	12
	QM, F5557		Right				30		11
	QM, F7033		Right						10+
	AM, F54724		Left		26				
	AM, F54725		Left				27	13	10
	AM, F54726		Right				29	12	10
<i>P. naracoortensis</i>	SAM, P17856		Right	96	22	9		11	9
	QM, F2769		Left		23				
	SAM, P18185		Right		21	10			
<i>G. victoria</i>	NMV, W6676		Left	98	17	7	17	7	6
			Right	99	17	7	17	7	6
<i>G. scheepmakeri</i>	NMV, R8054		Left	93	17	7	14	7	6
			Right	93	17	6	14	7	6
<i>L. ocellata</i>	SAM, B11482	♂	Left	72	15	7	18		
			Right	72	15	7	17		
	SAM, B5039	♀	Right	77	16	7	17	10	6
	NMV, B9276		Left	74	15	7	17	9	6
<i>A. lathamii</i>			Right	74	16	7	17	9	6
	NMV, W5964		Left	87	16	6	16	8	6
			Right	87	16	7	16	8	6
	NMV, W4554		Left	89	15	6	14	8	7
			Right	89	15	6	15	8	6
	NMV, W4555		Left	89	15	6	16	8	6
<i>M. Reinwardt</i>			Right	90	15	6	17	8	6
	CSIRO, GALS 2		Left	76	14	6	15	7	6
			Right	76	14	6	14	7	5
<i>M. pritchardi</i>	CSIRO, GALS 3		Left	77	14	6	15	7	6
			Right	77	14	6	15	7	6
	USNM, 319634		Left		9	4	11	5	4
			Right	59	9	4	10	5	4

References

- BRODRICK, P. (1964).—Catalogue of fossil birds: Part 2. *Bull. Florida State Mus.* 8(3), 195-335.
- DE Vries, C. W. (1888a).—Australian ancestry of the crowned pigeon of New Guinea. *Proc. R. Soc. Qld* 5, 127-131, Plate VI.
- DE Vries, C. W. (1888b).—A glimpse of the Post-Tertiary avifauna of Queensland. *Proc. Linn. Soc. N.S.W.* (Ser. 2) 3, 1,277-1,292, Plate XXXV.
- DE Vries, C. W. (1889).—Additions to the list of fossil birds. *Proc. R. Soc. Qld* 6, 55-58, Plate IV.
- DE Vries, C. W. (1891).—Residue of the extinct birds of Queensland as yet detected. *Proc. Linn. Soc. N.S.W.* (Ser. 2) 6, 437-456, Plate XXIV.
- FRITH, H. J. (1962).—"The Mallee-Fowl." (Angus & Robertson; Sydney.)
- HARVEY, E. B., KAISER, H. E., & ROSENBERG, L. F. (1968).—"An atlas of the Domestic Turkey (*Meleagris gallopavo*) myology and osteology." (U.S. Atomic Energy Commission Div. Biol. & Med.)
- LONGMAN, H. A. (1945).—Fossil vertebrates from Gore Quarries. *Mem. Qld Mus.* 12, 164.
- LYNEKKE, R. (1891).—"Catalogue of the fossil birds in the British Museum Natural History." (London.)
- MASCHLANKA, Hildegard (1972).—Proportionanalyse von Hühnervögeln. *Z. wiss. Zool., Leipzig* 183(3/4), 206-252.
- SCARLETT, R. J. (1972).—Bones for the New Zealand archaeologist. *Canterbury Mus. Bull.* 4.
- SCHNELL, G. D. (1970).—A phenetic study of the suborder Lari (Aves). I. Methods and results of principal components Analyses. *Systematic Zoology* 19, 35-57.
- SUTTER, E. (1965).—Zum Wachstum der Grossfusshühner (*Alectura* und *Megapodius*). *Orn. Beob.* 62, 43-60.
- VAN TETS, G. F., & SMITH, Meredith J. (1974).—Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. III. Birds (Aves). *Trans. R. Soc. S. Aust.* 98(4), 225-227.